

Competition between *Anisopteromalus calandrae* and *Choetospila elegans* (Hymenoptera: Pteromalidae) at Different Parasitoid Densities on Immature Rice Weevils (Coleoptera: Curculionidae) in Wheat

BIRAN WEN¹ AND JOHN H. BROWER²

USDA-ARS, U.S. Grain Marketing Research Laboratory, 1515 College Avenue, Manhattan, Kansas 66502

Received November 30, 1993; accepted August 18, 1994

Competition between parasitoids was studied by exposing immature rice weevils, *Sitophilus oryzae* (L.), developing in wheat to *Anisopteromalus calandrae* (Howard) alone, *Choetospila elegans* Westwood alone, or both species together. With *A. calandrae* only, the emergence of *A. calandrae* progeny tended to peak near four or eight female parasitoids and parasitoid-induced mortality increased with increasing parasitoid numbers. With *C. elegans* only, parasitoid emergence increased, but parasitoid-induced mortality did not change with an increase in numbers of parasitoids. *A. calandrae* in combination with *C. elegans* produced similar reductions in rice weevil populations, as did *A. calandrae* alone. *C. elegans* alone was less efficient than *A. calandrae* alone at low parasitoid densities, but when numbers of *C. elegans* reached higher densities, rice weevil mortality was as great as that with *A. calandrae* alone. Under competitive conditions, the sex ratio (female percentage) of *C. elegans* was decreased by the presence of *A. calandrae*, but the sex ratio of *A. calandrae* was not affected by *C. elegans*. Competition reduced emergence of both *A. calandrae* and *C. elegans*; however, *A. calandrae* was clearly the dominant species when rice weevils were exposed to equal numbers of both species of parasitoids. © 1995

Academic Press, Inc.

KEY WORDS: *Anisopteromalus calandrae*; *Choetospila elegans*; parasitoid; biological control; competitive parasitism; rice weevil; *Sitophilus oryzae*; stored wheat.

INTRODUCTION

Interspecific competition among natural enemies of a given host can be of great importance in the application of biological control (Ehler, 1978; Lawton, 1986;

Hagvar, 1989; van Alebeek *et al.*, 1993). Competition among species of insect parasitoids or predators can influence the size and structure as well as the stability of insect communities (Mackauer, 1990). It is possible that interspecific competition among parasitoids could lead to reduced levels of overall parasitization and pest population regulation (e.g., Turnbull and Chant, 1961; Watt, 1965; Pschorn-Walcher, 1977; Ehler and Hall, 1982). However, coevolved parasitoids could minimize competition by niche differentiation or interspecific host discrimination and produce greater suppressive effects (DeBach, 1966; Huffaker *et al.*, 1976; Keller, 1984; Hagvar, 1989; van Alebeek *et al.*, 1993).

Two hymenopteran parasitoids in the family Pteromalidae, *Anisopteromalus calandrae* (Howard) and *Choetospila elegans* Westwood, are solitary ectoparasitoids. Both *A. calandrae* and *C. elegans* attack immature stages of several insect pests of stored products. Laboratory studies have shown the potential for suppressing populations of the rice weevil, *Sitophilus oryzae* (L.), in wheat by *A. calandrae* (Press *et al.*, 1984; Cline *et al.*, 1985; Press, 1992) and by *C. elegans* (Press, 1992). Both *A. calandrae* and *C. elegans* can affect populations of the maize weevil, *S. zeamais* Motschulsky, in corn (Williams and Floyd, 1971; Arbogast and Mullen, 1990). Several studies have been conducted on the bionomics of *A. calandrae* (Chatterji, 1955; Ghani and Sweetman, 1955; Press, 1988; Smith, 1992) and *C. elegans* (Loosjes, 1957; van den Assem and Kuenen, 1958; Sharifi, 1972; Almeida and Matioli, 1984). Wen *et al.* (1994) reported that in stored corn, *A. calandrae* was more efficient at parasitizing immature maize weevil than the smaller *C. elegans*, and under interspecific competition, the emergence and sex ratio (percentage female) of *C. elegans* were significantly reduced by the presence of *A. calandrae* but not vice versa. However, there are no reports on the competitive parasitism of the rice weevil in wheat by these two important parasitoids. Because differences in the physical properties of the two grains could alter the success of the parasitism, the competitive situation could also be affected.

¹ Present address: Department of Entomology, Biological Sciences Building, University of Georgia, Athens, Georgia 30602.

² To whom reprint requests should be addressed.

The purpose of this study was to investigate the competition between *A. calandreae* and *C. elegans* in stored wheat to determine whether these two parasitoids can coexist better in this commodity than in corn and to assess the implications of this information for augmentative release of these parasitoids. The rice weevil, *Sitophilus oryzae*, was chosen in this study because in wheat the rice weevil is the more serious pest insect (Champ and Dyte, 1976; Longstaff, 1981).

MATERIALS AND METHODS

This experiment was performed in a walk-in environmental growth chamber at $30 \pm 0.5^\circ\text{C}$, at $65 \pm 5\%$ RH, and for a 12:12-h (L:D) photoperiod. Insects used in this study were obtained from colonies maintained at the USDA laboratory (Savannah, GA). Rice weevils were reared on wheat in the laboratory for many years. The stock cultures of both *A. calandreae* and *C. elegans* were derived originally from farm-stored wheat in South Carolina. These two parasitoids were reared on the rice weevil, *S. oryzae*, in wheat for more than 4 years. The rearing conditions for these parasitoids were $28 \pm 0.5^\circ\text{C}$, $65 \pm 5\%$ RH, and 12L:12D. Newly emerged to 1-day-old parasitoids were obtained for this experiment by being aspirated from stock cultures and placed in empty jars for 1 day to allow for mating. One- to two-day-old female parasitoids were then used for the experiment.

About 3000 rice weevil adults of mixed age were added to 45 kg of soft red wheat (the moisture content of the wheat was $13.9 \pm 0.1\%$), which had been disinfested by freezing at -10°C , >4 weeks, sifted over an official USDA grain dockage sieve (No. D, openings $1/2 \times 1/32$ in.) to remove dockage, and equilibrated to room temperature. After 48 h, rice weevil adults were removed by sifting. Nineteen days after rice weevil infestation, wheat was mixed thoroughly, weighed into 450-g samples, and placed in 0.95-liter jars. The same day, mated female parasitoids were randomly selected by use of an aspirator and introduced to each jar. The

three treatment groups of female parasitoids were *A. calandreae* alone, *C. elegans* alone, and equal numbers of both species. Five densities of parasitoids (2, 4, 8, 16, and 32 female parasitoids) were used. In the combination treatments, half of the female parasitoids were composed of each species. After 4 days, the parasitoids were removed. Ten jars of infested wheat without parasitoids served as controls; all other treatments were replicated five times. At the time of emergence of F_1 parasitoids, wheat was sifted once a day to remove, identify, and count adult parasitoids. After the emergence of F_1 parasitoids ceased, the wheat was sifted once a week until 56 days after the initial rice weevil infestation to collect and count F_1 rice weevils.

In this study, the average number of rice weevils that emerged in the controls was used as the basis for host density in the treatments. In the absence of parasitoids, the average number (\pm SE) of F_1 rice weevils per jar was 146.2 ± 2.8 . Percentage of rice weevil emergence was then calculated by dividing the number of rice weevils emerged from the treatment by the average number of rice weevils in the controls. The percentage of parasitoid emergence was calculated by dividing the number of parasitoids emerged by the average number of rice weevils in the controls. Parasitoid-induced mortality (PIM) was due to superparasitism, host feeding, or unsuccessful parasitism (Pawson *et al.*, 1987) and was calculated as the difference between 100% and percentages of rice weevil emergence plus parasitoid emergence. The total number of rice weevils killed was estimated by subtracting the number of rice weevils that emerged in the treatments from the average number of rice weevils that emerged in the controls. Sex ratio of parasitoids was calculated by dividing the number of female parasitoid progeny by the total number of parasitoid progeny in each jar.

Statistical analysis. The effects of the female parasitoid number on percentage of parasitoid emergence, parasitoid-induced mortality, percentage of rice weevil emergence, and progeny sex ratio (percentage female)

TABLE 1
Effect of Parasitoid Density on Number of Rice Weevils Killed (\pm SE) When Exposed to *A. calandreae* and *C. elegans* Separately or in Combination

(Female) Treatment	Number of rice weevils killed at five parasitoid densities ^a				
	2	4	8	16	32
Ac ^b	102.8 \pm 3.9a	136.4 \pm 1.9a	140.6 \pm 1.3a	143.6 \pm 0.4a	142.4 \pm 0.3a
Ac + Ce	99.4 \pm 3.9a	134.4 \pm 2.0a	141.0 \pm 1.0a	144.4 \pm 0.7a	145.0 \pm 0.3b
Ce ^c	61.2 \pm 9.3b	113.4 \pm 4.4b	121.6 \pm 5.4b	144.2 \pm 0.4a	145.4 \pm 0.3b

^a Values in the same column followed by the same letter did not differ significantly ($P \geq 0.05$, Waller-Duncan *K* ratio *t* test; SAS Institute, 1988).

^b Ac, *Anisopteromalus calandreae*.

^c Ce, *Choetospila elegans*.

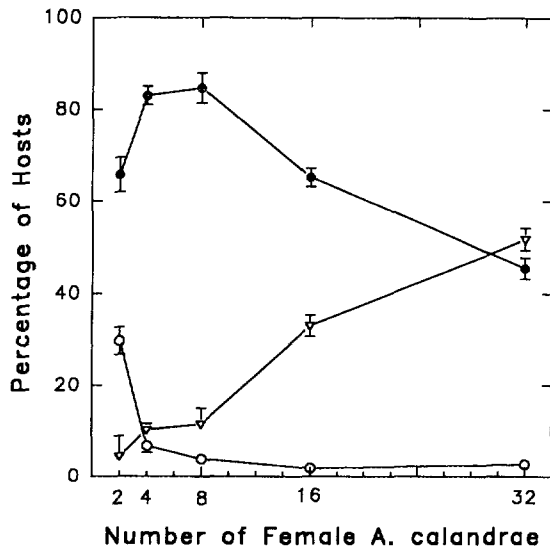


FIG. 1. Effect of *A. calandrae* density on percentage of parasitoid emergence (●), percentage of host emergence (○), and percentage of parasitoid-induced mortality (▽) (means \pm SE).

were analyzed by the General Linear Model (GLM) procedure (SAS Institute, 1988). Trends in response variables were tested by *t* tests of the slope estimates from linear regression. Nonlinear regression procedure (SAS Institute, 1988) was used to fit asymptotic equation for sex ratio of *A. calandrae*. Lack of fit test (Draper and Smith, 1981) was conducted to test model fitness. Analysis of variance (ANOVA) was used to analyze the effect of competition on parasitoid sex ratio and number of parasitoid emergence on classification variables (TRT, *A. calandrae* alone versus *A. calandrae* with *C. elegans* or *C. elegans* alone versus *C. elegans* with *A. calandrae*; species, *A. calandrae* versus *C. elegans*) after fitting any appropriate quantitative factors (e.g., NUMBER, the number of female parasitoids), and in the analysis the parasitoid sex ratio was transformed by using arcsine square root. Multiple comparisons of number of rice weevils killed were made using PROC ANOVA with the Waller-Duncan *K* ratio *t* test (SAS Institute, 1988).

RESULTS

Numbers of rice weevils killed by the three treatments are shown in Table 1. When *A. calandrae* was

used alone or when the two species were combined, numbers of rice weevils killed did not differ at any parasitoid density (except at 32 females). When *C. elegans* was released alone, at lower parasitoid densities, numbers of rice weevils killed were significantly lower than those in the higher two treatments. However, at 16 female *C. elegans*, the same result was obtained as when 16 *A. calandrae* were released alone or when the two species were combined. At 32 female parasitoids, *C. elegans* alone was even more effective in reducing rice weevil numbers than was *A. calandrae* alone (Table 1).

When *A. calandrae* was introduced at five densities, increasing parasitoid numbers greatly reduced rice weevil numbers and the calculated percentage of rice weevil emergence (Fig. 1; $t = 3.01$, $df = 1$, $P < 0.006$) and significantly increased the PIM (Fig. 1; $t = 12.61$, $df = 1$, $P < 0.005$). The percentage of *A. calandrae* emergence increased when up to eight female parasitoids were released, but thereafter decreased (Fig. 1) (GLM model, $Y = \text{NUMBER}^2$, $F = 40.04$, $df = 1, 23$, $P < 0.005$). The sex ratio (female percentage) of *A. calandrae* decreased with an increase in parasitoid numbers (Table 2) and can be represented by an exponential model: $Y = 31.52 + 49.59e^{-0.14X}$ (where *Y* is the sex ratio of *A. calandrae*; and *X* is the number of female *A. calandrae*) (regression, $F = 44.18$, $df = 3, 22$; lack of fit, $F = 0.47$, $df = 2, 20$, $P > 0.63$).

When *C. elegans* was introduced alone, the numbers and percentage of rice weevil emergence decreased as the number of parasitoids increased (Fig. 2; $t = 4.65$, $df = 1$, $P < 0.005$). The percentage of *C. elegans* emergence increased to a plateau between 16 and 32 female parasitoids (Fig. 2; $t = 5.03$, $df = 1$, $P < 0.005$). However, the PIM did not change with an increase in parasitoid numbers (Fig. 2; $t = 1.07$, $df = 1$, $P > 0.30$). The sex ratio (female percentage) of *C. elegans* was higher than that of *A. calandrae* (Table 2; GLM model; $Y = \text{SPECIES NUMBER NUMBER}^2$; Species, $F = 113.78$, $df = 1, 46$, $P < 0.0001$) and decreased linearly with increasing parasitoid numbers (Table 2; GLM model, $Y = \text{NUMBER}$, $F = 6.90$, $df = 1, 23$, $P < 0.02$).

When both *A. calandrae* and *C. elegans* were released together on rice weevil infested wheat, the percentage of *A. calandrae* emergence, the percentage of rice weevil emergence, and the PIM all had similar trends (Fig.

TABLE 2
Sex Ratio (Female Percentage \pm SE) of Parasitoid Progeny

Treatment	Number of female parasitoids introduced				
	2	4	8	16	32
Ac alone	69.2 \pm 5.6	59.4 \pm 2.6	45.5 \pm 2.8	39.3 \pm 3.0	30.7 \pm 3.8
Ce alone	80.2 \pm 3.0	75.4 \pm 2.4	77.2 \pm 1.8	73.4 \pm 1.8	71.7 \pm 1.7

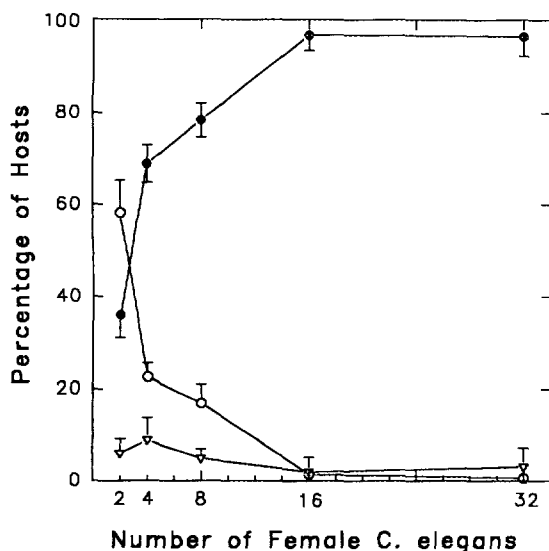


FIG. 2. Effect of *C. elegans* density on percentage of parasitoid emergence (●), percentage of host emergence (○), and percentage of parasitoid-induced mortality (▽) (means \pm SE).

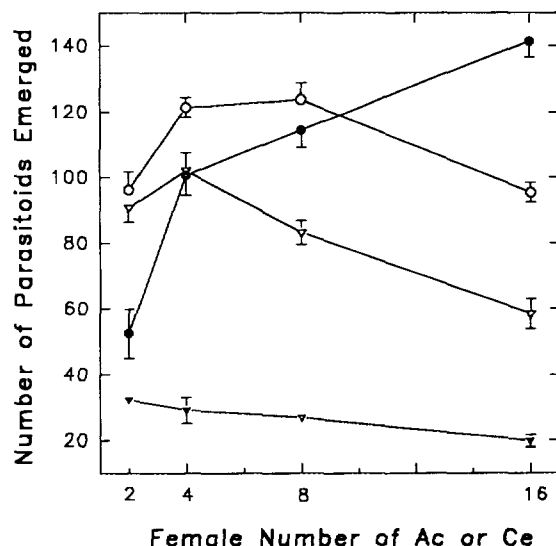


FIG. 4. Effect of competition on *A. calandrar* and *C. elegans* emergence at four parasitoid densities: *A. calandrar* alone (○), *C. elegans* alone (●), *A. calandrar* in the presence of *C. elegans* (▽), *C. elegans* in the presence of *A. calandrar* (▼) (means \pm SE).

3) as when *A. calandrar* was released alone (Fig. 1). However, the percentage of *C. elegans* emergence decreased with an increase in the number of released parasitoids (Fig. 3; $t = 5.27$, $P < 0.0001$). The overall percentage of *A. calandrar* was 2.8-fold of that of *C. elegans* (Fig. 3; GLM model, $Y = \text{SPECIES NUMBER}^2$; Species, $F = 237.92$, $df = 1, 46$; $P < 0.0001$). Percentage of rice weevil emergence significantly decreased with an increase in the number of

parasitoids released (Fig. 3; $t = 3.50$, $df = 1$, $P < 0.002$). PIM also increased with increasing parasitoid density in the combined release (Fig. 3; $t = 12.02$, $df = 1$, $P < 0.005$).

Interspecific competition. The effects of interspecific competition were assessed by comparing the number of parasitoid progeny resulting from equal numbers of each species of parasitoid in the presence and absence of competition. For example, two female *A. calandrar* were compared to the combination of two female *A. calandrar* plus two female *C. elegans*. Using this scheme, these species were compared at four densities. The numbers of both *A. calandrar* and *C. elegans* that emerged decreased when in competition with each other (Fig. 4). The average *A. calandrar* emergence decreased by 23.44% when in competition with *C. elegans* (Table 3; TRT, $F = 67.68$, $df = 1, 32$; $P < 0.0005$). However, the average *C. elegans* emergence decreased by 73.61% when in competition with *A. calandrar* (Table 3; TRT, $F = 551.78$; $df = 1, 32$; $P < 0.0005$). The significance of the NUMBER factor indicates that averaged over the two treatments, the means of parasitoid emergence at four parasitoid densities were significant, and the significance of the interaction term ($T \times N$) indicates that the difference between the two treatments was not constant at all parasitoid densities.

The effects of interspecific competition on parasitoid sex ratio were compared using the same design as that above (Fig. 5). The sex ratio of *A. calandrar* did not differ significantly when alone or in competition with *C. elegans* (Table 4; TRT, $F = 0.60$, $df = 1, 32$, $P > 0.45$). The nonsignificance of the interaction term in *A. calandrar* indicates that the responses can be consid-

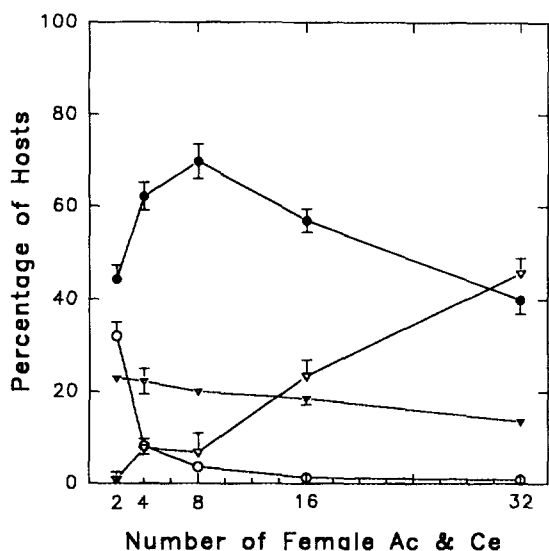


FIG. 3. Effect of parasitoid density on parasitism of rice weevils in wheat when both *A. calandrar* and *C. elegans* are present: percentage of weevil emergence (○), percentage of *A. calandrar* emergence (●), percentage of *C. elegans* emergence (▼), percentage of parasitoid-induced mortality (▽) (means \pm SE).

TABLE 3

Analysis of Variance of Effect of Interspecific Competition (TRT) and Parasitoid Density (NUMBER) on Number of Parasitoid Emergence

Source	df	<i>A. calandrae</i>			<i>C. elegans</i>		
		MS	F	P	MS	F	P
Model	7	2184.11	22.55	0.0001	11106.40	108.37	0.0001
TRT	1	6553.60	67.68	0.0001	56550.40	551.78	0.0001
NUMBER	3	2243.87	23.17	0.0001	2609.67	25.46	0.0001
T × N	3	667.87	6.90	0.001	4455.13	43.47	0.0001
Error	32	96.84			102.49		

ered parallel. However, the percentage of *C. elegans* females decreased significantly when in competition with *A. calandrae* compared to *C. elegans* alone (Table 4; TRT, $F = 12.34$; $df = 1,32$, $P < 0.005$).

DISCUSSION

When only *A. calandrae* was released, increasing parasitoid density produced a quadratic effect on parasitoid progeny emergence. The decline in parasitoid emergence at higher parasitoid densities was probably due to superparasitism because there was a corresponding increase in PIM of the host (Fig. 1). In wheat, the trends of *A. calandrae* emergence and PIM were similar to those reported earlier for corn (see Wen *et al.*, 1994). However, the percentage of weevil emergence was higher in corn than in wheat, which indicated that *A. calandrae* was more efficient in wheat than in corn in reducing *Sitophilus* species. The sex ratio of *A. calandrae* decreased with an increase in parasitoid density. This decrease may result from either the perception of chemical traces left by other females on the patch of hosts (e.g., Viktorov and Kochetova, 1973) or parasitoids more often encountering other female parasitoids while ovipositing at higher parasitoid densities (e.g., Wylie, 1976, 1979; King, 1989) because females may regulate sex ratio in relation to the number of other females colonizing a patch (Comins and Wellings, 1985). Hassell *et al.* (1983) also presented data from a number of laboratory studies which demonstrated that sex ratio (female percentage) was a decreasing function of the female parasitoid density. In addition, superparasitism and differential mortality in superparasitized hosts could also be important factors contributing to the decline in female percentage (e.g., van Dijken *et al.*, 1993) because superparasitism often yields evidence for competitive superiority of one of the sexes (King, 1987).

When *C. elegans* was released alone, the percentage of weevil emergence in corn was much higher than it was in wheat, indicating that the very small *C. elegans* was more efficient in wheat than in corn. They were probably affected by the large size and the hardness of

the corn kernels. van den Assem and Kuenen (1958) reported that *C. elegans* found larvae within grain by detection of mechanical stimuli set up by larval activity and when a kernel of wheat in which *C. elegans* had oviposited was opened, a weevil larva was always found near the surface where oviposition by the parasitoid had taken place. Corn kernels are much larger than wheat kernels, and the distance between larvae in corn kernels and the surface of the kernel can be much greater than that in wheat kernels. Thus, the larvae inside wheat kernels may be easier for *C. elegans* to detect through mechanical stimuli of host larvae or much easier to reach with a short ovipositor than in corn, and parasitism was much higher in wheat than in corn. In addition, the emergence of *C. elegans* was greatly enhanced in wheat compared to corn. A plateau of *C. elegans* emergence was reached at 16 females, and the emergence of *C. elegans* did not increase fur-

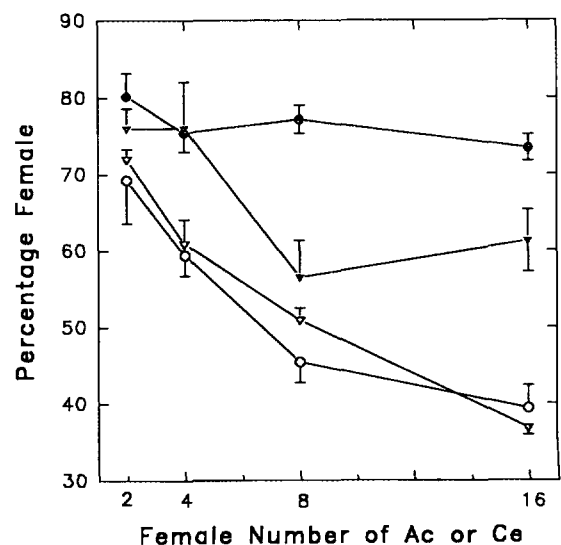


FIG. 5. Effect of competition on sex ratio (percentage female) of *A. calandrae* and *C. elegans* at four parasitoid densities: *A. calandrae* alone (○), *C. elegans* alone (●), *A. calandrae* in the presence of *C. elegans* (▽), *C. elegans* in the presence of *A. calandrae* (▼) (means \pm SE).

TABLE 4

Analysis of Variance of Effect of Interspecific Competition (TRT) and Parasitoid Density (NUMBER) on Parasitoid Sex Ratio (Female Percentage)

Source	df	<i>A. calandray</i>			<i>C. elegans</i>		
		MS	F	P	MS	F	P
Model	7	0.09	18.65	0.0001	0.09	6.03	0.0002
TRT	1	0.003	0.60	0.45	0.18	12.34	0.0013
NUMBER	3	0.21	42.77	0.0001	0.09	5.85	0.0026
T × N	3	0.003	0.54	0.66	0.06	4.11	0.014
Error	32	0.01			0.45		

ther when 32 females were released. This is because there were few additional available hosts for any more *C. elegans* at 32 parasitoids. However, there was no decrease in *C. elegans* emergence when *C. elegans* density was 32. The high percentage of *C. elegans* emergence with no decrease and the low PIM at any parasitoid density indicated that little superparasitism existed, and *C. elegans* probably discriminated between parasitized and unparasitized hosts, which would be a great advantage for mass rearing and mass releasing. Wen *et al.* (1994) also reported low PIM and increasing emergence of *C. elegans* in parasitizing maize weevils in corn, although in corn the percentage of *C. elegans* emergence was not as high. Thus releasing a high density of *C. elegans* would not decrease the emergence of *C. elegans* progeny by inducing superparasitism. When *C. elegans* was used alone, the number of rice weevils killed at lower *C. elegans* densities (2, 4, and 8 female *C. elegans*) was significantly lower than that with *A. calandray* alone or with the two species combined. However, at 16 parasitoids, no difference was detected (Table 1). This indicates that although individual *A. calandray* was more efficient at parasitizing the rice weevil in wheat than was *C. elegans*, the same suppressive effect could be obtained as with *A. calandray* alone because of low intraspecific competition in *C. elegans*, when *C. elegans* density reached a certain level. In fact, 32 female *A. calandray* produced less rice weevil mortality than 32 female *C. elegans* because of intraspecific competition in *A. calandray*.

When releases of *A. calandray* and *C. elegans* were combined, overall emergence of *A. calandray* was almost three times that of *C. elegans*. Thus *A. calandray* was the dominant species in wheat, a finding similar to the one reported by Wen *et al.* (1994) for corn. In wheat, the emergence of both *C. elegans* and *A. calandray* was reduced by the presence of each other. The population suppression by competition can result from some action or process between the immature stages or from some action of the adult wasp that affects larval survival (Mackauer, 1990). For example, superior competitor species could kill inferior competitor species at immature stages by physically attacking; by injecting

during oviposition a substance or substances toxic to other parasitoid species eggs or embryos, a female could gain control of an already parasitized host and make it suitable for the development of her own offspring (Mackauer, 1990).

The results of this experiment indicate that there is direct competition between these two parasitoids, even though combining the two species had similar effect as *A. calandray* alone in suppressing rice weevil populations. Competition reduced emergence of both *A. calandray* and *C. elegans*, but *C. elegans* suffered a greater reduction than *A. calandray*. Thus combining the two species is not recommended for controlling the rice weevil in wheat. Although *C. elegans* was almost always the loser in competition, when it was alone (especially at higher parasitoid density) *C. elegans* sufficiently suppressed rice weevils. In wheat, therefore, *A. calandray* or *C. elegans* could be chosen for suppressing rice weevil populations. Press (1992) reported that in wheat *A. calandray* and *C. elegans* were equally effective against rice weevil populations occurring near the surface of a grain mass. However, *A. calandray* did not readily move downward to parasitize *S. oryzae* hosts confined to the bottom of 2.2-m columns of wheat (Press, 1988), so because of better downward penetration through wheat by *C. elegans*, *C. elegans* might give a higher level of weevil parasitization beneath the surface (Press, 1992). Thus in commercial use in bulk wheat, *C. elegans* is probably a better choice because of the depth of grain on commercial storages in which many infested kernels are likely to occur deep within a grain mass.

ACKNOWLEDGMENTS

We thank Jim Thorpe and Rachel Potter, biological technicians, for technical help; Victor Chew (USDA-ARS, University of Florida, Gainesville) for statistical advice; and Michael Mullen, David K. Weaver (Stored-Product Insects Research and Development Laboratory, USDA-ARS, Savannah, GA) and Gerrit W. Cuperus (Department of Entomology, Oklahoma State University, Stillwater) for reviewing the manuscript.

REFERENCES

- Almeida, A. A., and Mاتيoli, J. C. 1984. Ocorrencia de *Choetospila elegans* Westwood, 1874 (Hym., Pteromalidae) como parasito de *Sitophilus oryzae* (Linnaeus, 1763) (Col., Curculionidae). *An. Soc. Entomol. Brasil* **13**, 107–115.
- Arbogast, R. T., and Mullen, M. A. 1990. Interaction of maize weevil (Coleoptera: Curculionidae) and parasitoid *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae) in a small bulk of stored corn. *J. Econ. Entomol.* **83**, 2462–2468.
- Champ, B. R., and Dyte, C. E. 1976. Report of the FAO global survey of pesticide susceptibility of stored grain pest. *FAO Plant Production and Protection Serial No. 5*, Rome.
- Chatterji, S. 1955. Studies on the biology of *Aplastomorpha calandrae* Howard (Insecta: Hymenoptera: Chalcidae) parasitic on some storage pests. *Proc. Zool. Soc.* **8**, 11–23.
- Cline, L. D., Press, J. W., and Flaherty, B. R. 1985. Suppression of the rice weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae), inside and outside of burlap, woven polypropylene, and cotton bags by the parasitic wasp, *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae). *J. Econ. Entomol.* **78**, 835–838.
- Comins, H. N., and Wellings, P. W. 1985. Density-related parasitoid sex-ratio: Influence on host-parasitoid dynamics. *J. Anim. Ecol.* **54**, 583–594.
- DeBach, P. 1966. The competitive displacement and coexistence principles. *Annu. Rev. Entomol.* **11**, 183–212.
- Draper, N. R., and Smith, H. 1981. "Applied Regression Analysis," Wiley, New York, pp. 33–40.
- Ehler, L. E. 1978. Competition between two natural enemies of mediterranean black scale on olive. *Environ. Entomol.* **7**, 521–523.
- Ehler, L. E., and Hall, R. W. 1982. Evidence for competitive exclusion of introduced natural enemies in biological control. *Environ. Entomol.* **11**, 1–4.
- Ghani, M. A., and Sweetman, H. L. 1955. Ecological studies on the granary weevil parasite, *Aplastomorpha calandrae* (Howard). *Biologia* **1**, 115–139.
- Hagvar, E. B. 1989. Interspecific competition in parasitoids, with implications for biological control. *Acta. Entomol. Bohemoslov.* **86**, 321–335.
- Hassell, M. P., Waage, J. K., and May, R. M. 1983. Variable parasitoid sex ratios and their effect on host-parasitoid dynamics. *J. Anim. Ecol.* **52**, 889–904.
- Huffaker, C. G., Simmonds, F. J., and Laing, J. E. 1976. Theoretical and empirical basis of biological control. In "Theory and Practice of Biological Control" (C. B. Huffaker and P. S. Messenger, Eds.), pp. 41–78. Academic Press, New York.
- Keller, M. A. 1984. Reassessing evidence for competitive exclusion of introduced natural enemies. *Environ. Entomol.* **13**, 192–195.
- King, G. H. 1987. Offspring sex ratio in parasitoid wasps. *Q. Rev. Biol.* **62**, 367–396.
- King, B. H. 1989. A test of local mate competition theory with a solitary species of parasitoid wasp, *Spalangia cameroni*. *Oikos* **54**, 50–54.
- Lawton, J. H. 1986. The effect of parasitoids on phytophagous insect communities. In "Insect Parasitoids" (J. Waage and D. Greathead, Eds.), pp. 265–287. Academic Press, London.
- Longstaff, B. C. 1981. Biology of the grain pest species of the genus *Sitophilus* (Coleoptera: Curculionidae): A critical review. *Protect. Ecol.* **3**, 83–130.
- Loosjes, F. E. 1957. Ervaringen met *Choetospila elegans* (Westw.) (Hymenoptera, Pteromalidae), een parasiet van enige soorten voorraad-insecten. *Entomol. Ber. Amsterdam* **17**, 74–76.
- Mackauer, M. 1990. Host discrimination and larval competition in solitary endoparasitoids. In "Critical Issues in Biological Control" (M. Mackauer, L. E. Ehler, and J. Roland, Eds.), pp. 41–62. Intercept Ltd., Andover, UK.
- Pawson, B. M., Petersen, J. J., and Holtzer, T. O. 1987. Competitive parasitism of house fly pupae (Diptera: Muscidae) by *Muscidifurax zaraptor* and *Urolepis rufipes* (Hymenoptera: Pteromalidae). *J. Med. Entomol.* **24**, 66–70.
- Press, J. W. 1988. Movement of a weevil parasitoid, *Anisopteromalus calandrae* (Howard), within a column of wheat in relation to host location. *J. Agri. Entomol.* **5**, 205–208.
- Press, J. W. 1992. Comparative penetration efficacy in wheat between the weevil parasitoids *Anisopteromalus calandrae* and *Choetospila elegans* (Hymenoptera: Pteromalidae). *J. Entomol. Sci.* **27**, 154–157.
- Press, J. W., Cline, L. D., and Flaherty, B. R. 1984. Suppression of residual populations of the rice weevil, *Sitophilus oryzae*, by the parasitic wasp, *Anisopteromalus calandrae*. *J. Ga. Entomol. Soc.* **19**, 110–113.
- Pschorn-Walcher, H. 1977. Biological control of forest insects. *Annu. Rev. Entomol.* **22**, 1–22.
- SAS Institute 1988. SAS/STAT user's guide, release 6.04. SAS Institute, Cary, NC.
- Sharifi, S. 1972. Radiographic studies of the parasite *Choetospila elegans* on the maize weevil, *Sitophilus zeamais*. *Ann. Entomol. Soc. Am.* **65**, 852–856.
- Smith, L. 1992. Effect of temperature on life history characteristics of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae) parasitizing maize weevil larvae in corn kernels. *Environ. Entomol.* **21**, 877–887.
- Turnbull, A. L., and Chant, D. A. 1961. The practice and theory of biological control of insects in Canada. *Can. J. Zool.* **39**, 697–753.
- van Alebeek, F. A. N., Rojas-Rousse, D., and Leveque, L. 1993. Interspecific competition between *Eupelmus vuillei* and *Dinarmus basalis*, two solitary ectoparasitoids of Bruchidae larvae and pupae. *Entomol. Exp. Appl.* **69**, 21–31.
- van den Assem, J., and Kuenen, D. J. 1958. Host finding of *Choetospila elegans* Westw. (Hym. Chalcid.) a parasite of *Sitophilus granarius* L. (Coleopt. Curcul.). *Entomol. Exp. Appl.* **1**, 174–180.
- van Dijken, M. J., van Stratum, P., and van Alphen, J. M. 1993. Superparasitism and sex ratio in the solitary parasitoid *Epidinocarsis lopezi*. *Entomol. Exp. Appl.* **68**, 51–58.
- Viktorov, G. A., and Kochetova, N. I. 1973. The role of trace pheromones in regulating sex ratio in *Trissolcus grandis* (Hymenoptera, Scelionidae). *Zhurnal. Obshchei Biologii* **34**, 556–562.
- Watt, K. E. F. 1965. Community stability and the strategy of biological control. *Can. Entomol.* **97**, 887–895.
- Wen, B., Smith, L., and Brower, J. H. 1994. Competition between *Anisopteromalus calandrae* and *Choetospila elegans* at different parasitoid densities on immature maize weevil in corn. *Environ. Entomol.* **23**, 367–373.
- Williams, R. N., and Floyd, E. H. 1971. Effect of two parasites, *Anisopteromalus calandrae* and *Choetospila elegans*, upon populations of the maize weevil under laboratory and natural conditions. *J. Econ. Entomol.* **64**, 1407–1408.
- Wylie, H. G. 1976. Interference among females of *Nasonia vitripennis* (Hymenoptera: Pteromalidae) and its effect on the sex ratio of their progeny. *Can. Entomol.* **108**, 655–661.
- Wylie, H. G. 1979. Sex ratio variability of *Muscidifurax zaraptor* (Hymenoptera, Pteromalidae). *Can. Entomol.* **111**, 105–107.